TERMITE MOUNDS.

BY THE LATE N. ANNANDALE, D.Sc., F.R.S., C.I.E.

Director, Zoological Survey of India. (With 4 text figures.)

(A lecture delivered at the eleventh meeting of the Indian Science Congress,

Bangalore: January 15th, 1924.)

You all are familiar with the earthen mounds commonly called ant-hills, which form so conspicuous a feature of the landscape in some parts of India (1). In spite of their popular name these mounds are built not by true ants but by termites, which are popularly called white-ants. The names, however, are misleading, for in structure and life-history the termite differs from the ant almost as much as either does from a beetle or a butterfly; its internal anatomy is different, its mouth-parts and legs are differently constructed, its body is not covered with a hard integument like that of the ant and its wings, if it has wings, are of quite a different pattern, the so-called veins never forming a network as they do in the ants and their allies. Moreover, the ant comes out of its egg as a helpless grub and undergoes a complete metamorphosis, whereas the termite is hatched active and not unlike the adult.

Ants and termites, nevertheless, have been confused in many countries, mainly on account of a curious similarity in their social systems. Both live in large communities in which the great majority of individuals are without wings, but numbers of winged individuals are produced periodically and issue from the nest in swarms. This fact, to the superficial observer at any rate, is perhaps the most striking point in the life-history of ants and termites, for their social system differs from that of any human community in that different individuals are adapted for different services, not by training or descent but by profound anatomical differences. The offspring of a single female are not all alike but differ in shape, size and structure to such an extent that it is often difficult to believe them in any way related one to another. The winged forms are the young males and females, which leave the nest to found new communities. In each community the service of replenishing the population is confined to a few individuals, often to a single pair, while the vast majority of the population are practically sexless, In most termites and in many ants these neuter individuals, which never have wings, are further subdivided into two castes, that of the workers and that of the soldiers. Things are often still more complicated and there may be two or more subcastes of workers, while among the most primitive termites there is little or no difference between workers and females. Further, in these primitive forms (and also in some of higher grade) the soldiers and even the workers are at least potential males and females.

All termites do not build mounds. The primitive forms to which I have alluded eat passages and galleries in dead wood and apparently have no permanent abode. Other species burrow in the earth, construct nests in dead logs or affix them to trees. The number of species which do build mounds in India is apparently small and all of them seem to be closely related and to belong to the genus *Odontotermes*. This is not so, however, in other countries.

In all our Indian mound-builders the three castes—the royal caste as it is called, the working caste and the military caste—are quite distinct, each physically incapable of performing any function but its own. The sole duty of the

⁽¹⁾ The absence of termite mounds from the reighbourhood of Calcutta and other parts of the lower Gangetic delta is a noteworthy fact. It is possibly due to the high level of the sub-soil water.

royal caste is the production of fertile eggs, the sole duty of the military caste is to guard the community and its abode against external enemies, while the workers build and forage and cultivate, act as scavengers and tend their parents and the young of their common mother. It is impossible here to give any account of the strange complexities which occur in some termite communities, but we may consider the three castes of the mound-builders in a little more detail.

The wings of the young males and females when they issue from the nest are ample but rather feeble. The two sexes differ little in external characters and are often hard to distinguish. Both males and females are at first active and apparently able to feed and look after themselves. Feeble as are their wings in appearance and delicate in structure, they are often capable of a flight of several miles. After one flight their wings drop off. The vast majority of the winged individuals of each community perish within a short time of leaving t, falling victims by the thousand to insectivorous birds and lizards, toads, jackals, cockroaches and especially predaceous ants, all of which devour them greedily. Only a few pairs, which have survived the perils of their flight and been able to mate, survive and, concealing themselves in crevices or burrowing under ground, proceed to found new communities. In their retreat a curious change comes over the female. She grows more and more unwieldy and her body swells up until it is altogether disproportionate to her head and legs and enormously greater than that of her mate, who retains his elegant shape with little alteration. The only work the pair are capable of doing is that of reproduction and the female pours out her eggs literally by the million, guarded by her soldier children and fed and tended by the proletariat of which she Her offspring often equals or exceeds the population of a is the mother. great city.

There is one point I should make clear before going any further. We call the male and the female termite the king and queen, but there is no evidence of any kind that they rule or govern the community: they are merely its father and its mother in the most literal sense. In all the Indian mounds I have examined I have found a single king and queen or sometimes a queen alone whose mate had died, but in some species there are commonly several pairs of true males and females, while in some the workers possess the mysterious power of raising up from among the young of their own caste supplementary queens, which never have complete wings but are capable of laying eggs, should any accident happen to their mother. This power, however, is not possessed by the common mound-builders of India. I have found by repeated experiment (1) that if the mound be destroyed and the royal pair removed, the workers reconstruct the edifice, and that this may be done at least once again if the new structure be again destroyed. The life of the community, however, is only that of the workers and never lasts for more than eight or nine months, although the queen if undisturbed continues to live and lay eggs for much longer, probably for at least ten years in some forms, and as long as she remains productive the community persists. The so-called king and queen of each mound are prisoners for life, quite incapable of looking after themselves and dependent on their children for food.

The majority of these children are workers condemned to a life of toil, blind, soft, much smaller even than their father, but with all their instincts concentrated on their work and possessed of a communal sense of responsibility far beyond that of the most altruistic human society. They feed their parents, carry away the eggs laid by their mother; they build, repair and enlarge the mound, they tend the gardens of the community, they forage abroad, they work

⁽¹⁾ This refers particularly to Odontotermes obesus, both the typical form and the variety oculatus.

n perfect unison and build up structures that seem to exhibit the most advanced knowledge of mechanics; but there is no one to give them orders, no one standing over them with a whip, no apparent means of communication, even, between them. Their jaws are their only tools, their saliva their only means of con-

solidating their work.

The soldiers of a large mound, though less numerous than the workers, form a huge army. Their weapons are their jaws, their defence the hard integument of their head; their bodies are soft as those of their sisters the workers. and they take good care to keep them under cover. In different kinds of termites the jaws of the soldiers are developed differently; in the Indian moundbuilders they form a pair of powerful forceps, fit for decapitating an insect foe or for wounding larger enemies.

So much for the inhabitants of the mounds, the structure and object of which we must now consider. Some have believed them to be mere rubbish heaps and this I think is true of one type of mound. On a recent visit to the Andaman Islands(1) I noticed on the jungle-floor numerous heaps of yellow clay which contrasted strongly with the black leaf-mould. They were not more than three feet high, had about the same diameter and were mere formless masses. On investigation I discovered that they were formed by termites, which had brought up the unctuous clay from below the deep layer of leaf-mould. The mounds were nearly solid with only a few narrow passages and contained no large chambers of any sort. They did not differ essentially except in being more solid from the rubbish heaps of earth often made among the roots of fig trees by Odontotermes tex, one of our commonest burrowing forms in Peninsular India.

It is not of simple mounds of this sort that I wish to speak to-night, but of the much more complex structures which serve primarily as forming houses

for certain species of fungi cultivated by the termites.

I will first describe the structure, external and internal, of the type of mound commonest in India. It is that built by Redemann's Termite (O. redemanni), a species common in Cevlon and South India. Externally its figure is that of a sharply pointed cone with or without supplementary pinnacles of the same shape. The cross-section is thus circular, often with smaller circles round a large central circle. The height may be six feet or more. The external surface is rough, but, so far as my own observations go, there are never any apertures in it when it is fresh, except at swarming-time when special vents are opened for the egress of the winged adults, and closed again immediately they have come out. This, however, is a point to which I will have to return later. If we break open the mound, we find that it is extremely hard. The mass as a whole is solid, but scattered through it are numerous domed chambers connected together by elaborate but narrow passages. Broader vertical shafts can also be distinguished, connected with these passages but blind at their upper extremity. The internal walls of the domed chambers are beautifully smooth, almost polished, and each contains a brown, spongy mass. This, as we shall see, is the actual fungus-garden. Low down in the mound, a little above ground-level and as a rule a little to one side, there is a single chamber, also domed, but lower and narrower and with rougher walls. It is, moreover, surrounded by a more elaborate system of passages. This is the royal chamber in which the king and queen are imprisoned. The passages round it are far too narrow for their exit and are used partly for the removal of the eggs, partly to allow the workers to approach the king and queen and partly as guard-chambers in

⁽¹⁾ Professor Silvestri has identified workers and soldiers of this termite as This is remarkable in view of what I have to say later Odontotermes obesus. on about the two types of mounds built by two different varieties of this species. Possibly males and females of the Andaman form would show some racial peculiarity.

which a large body of soldiers is always on duty. By far the greater part of the mound is thus devoted to cultivation, which is carried out in numerous small plots or gardens.

Sometimes mounds of this type are solitary, but the commonest of all our Indian mound-builders (O. obesus) as a rule builds a little group of smaller but otherwise similar mounds (fig. 1), which may coalesce into a single conical mass as the community increases in numbers and extends its building operations. The different mounds in the group are connected together under ground and the royal chamber is in one of them.



Fig. 1.

Mounds of Odontotermes obesus typicus (from the "Records of the Indian Museum").

Although the typical *O. obesus* builds a conical mound with many internal fungus-gardens, there is another variety of the species which builds a totally different kind of mound. The only physical difference that has been observed between the two varieties is that the males and females of the one which builds a conical mound have smaller eyes. No difference at all has been detected between the blind workers and soldiers.

The mound (fig. 2) of the large-eyed variety of this species is not conical but consists of a comparatively small central mass of somewhat irregular shape and surrounded by vertical buttresses as high as itself but very narrow. The cross-section is, therefore, star-shaped instead of circular. Each of the buttresses ends above in a sharp peak or in several peaks and the mound as a whole is usually of much the same size as that of *O. redemanni*.

The internal arrangement is, however, quite different. The buttresses are hollow and empty, while the central core is mainly solid but contains wide vertical passages, which are also empty. This part of the mound is regularly patrolled by bodies of workers and soldiers but is not used for cultivation. The whole of the base, however, is one great garden-chamber, shaped something like a limestone cave with stalactites and stalagmites and partially separated into two or several storeys by incomplete horizontal floors. This chamber contains a single large fungus-garden of much the same shape as itself.

We may call mounds of this type unilocular, while those of the typical O.

obesus and of O. redemanni may be called multilocular.

Some observers have maintained that the mounds of Indian termites are ventilated by a complex system of air-shafts opening on the surface by funnel-shaped apertures, but, so far as I have been able to see myself, this is a complete error of observation. Apertures and shafts (fig. 1) often appear in old mounds, especially in those of conical form, but they are always due to accident and will

be found on examination to be carefully blocked up below and to have no communication with the rest of the nest. Any hole in the external surface of the mound is, in fact, a danger as giving access to predaceous ants, which seem to be the chief enemy of the termite, and it is of the utmost importance in the cultivation of fungi that the temperature and moisture should be kept equable inside the mound, an end achieved by the solid earthen walls, which are bad conductors of heat, and possibly by the cushions of air in the vertical shafts and buttresses.

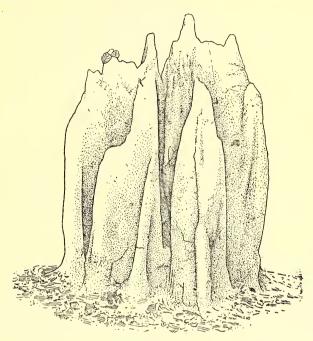


Fig. 2.

Mound of Odontotermes obesus oculatus (from the "Records of the Indian Museum").

So far as I can discover from the literature of the subject (which, however, is not very detailed), the great majority of termite mounds in all tropical countries belong in their internal structure to one or other of the two types described above, the multilocular being much more common than the unilocular. Mounds of the former type often reach a gigantic size. These are of course differences, and in detail, and some of the smaller kinds of mounds appear to be mere nests, containing chambers and passages devoid of gardens; for all termites are not cultivators.

In external shape the mounds of different species of termite exhibit great variety, though in each species or variety shape seems to be fairly constant. In India, so far as I can discover, only the conical form and the buttressed form have been figured or described, but, especially in tropical Africa and Australia, there are many peculiar exotic forms. One of these, which is probably (at any rate in some species) a mere nest, is that of a mushroom or umbrella, sometimes many-tiered like the ceremonial umbrellas of the potentates of the Far East. Mounds of this form are rarely of any great size. They are constructed by widely different termites in both Africa and Australia,

Another form of mound is that of a pillar or column, sometimes of great height. It appears to be merely a modification of the conical mound.

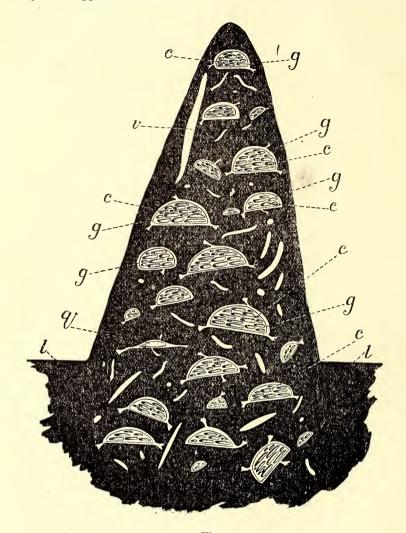


Fig. 3.

Vertical section of a mound of Odontotermes redemmani(Conical, multi-locular Diagrammatic).

c, fungus-comb. g, garden-chamber. l, ground-level.

q, queen in royal chamber. v, vertical shaft.

Strangest of all, however, is the "meridian" mound built in Australia by *Hamitermes meridionalis*. This termite inhabits the hot, dry, open plains of Northern Queensland. Its mound has the form of a high, narrow dyke, compressed in one direction and with a single long horizontal axis. One face is

convex, the other concave. The convex face is exposed to the rising sun, the concave face to the setting sun, for the long axis always points due north and south, so that the full force of the midday sun never strikes any part of the mound except the narrow ridge-like summit.

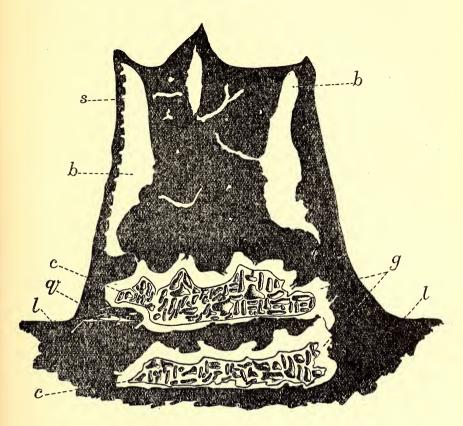


Fig. 4.

Vertical section of a mound of Olontotermes obesus var. oculatus (Buttressed, unilocular Diagrammatic).

b, hollow of buttress. c, fungus-comb. g, garden-chamber.

l, ground-level. q, queen in royal chamber. s, cavity for soldier on guard during the building of the mound.

It is clear that the shape and orientation of the meridian mound is correlated with meteorological phenomena. This mound is constructed and placed in such a way that moisture is conserved so far as possible and that over-heating is avoided. I believe that the form of the mound in different species has always some significance of the kind. I cannot suggest any particular advantage of the high columnar form of some mounds, unless it be to enable the upper parts to emerge from dense surrounding vegetation. The umbrella form probably has the function its name suggests, the hemispherical cap or caps on the top preserving the nest from heavy rain. Both the conical form and the buttressed

form have certainly this function, which is better served in the latter. Rain runs off easily from a cone but the water is apt to lodge in small cavities on the surface and especially in the burrows of various insects (¹) and spiders with which the outer wall of termite mounds is often pitted. Funnel-shaped openings are thus produced giving entrance into garden-chambers, but as these chambers are numerous and can be readily isolated by blocking up the narrow passages leading to them, no great harm is done. In the buttressed mounds on the other hand definite passages for the removal of rain-water are formed between the buttresses and it is only in very old and dilapidated mounds of this shape that breaches are formed by the action of water on the surface or in the burrows in the wall.

The next point we have to consider in this rapid survey is the way in which the mound is built. My own observations on this point refer to the two varieties of Odontotermes obesus, but there is no reason to think that there is any fundamental difference in other species. New mounds are constructed as a rule only in the wet season, at the beginning of which, in eastern India, O. obesus swarms. They are built mainly at night and work ceases shortly after sunrise, unless the weather be dull and damp. The first evidence that a new mound is in the building is the appearance of a crater-shaped hole in the ground, but this can only be seen at night. Before the crater appears the community has been formed underground and the progeny of its queen are already numerous. Round the hole a rampart is rapidly built up by the workers, each of which carries up in its mouth a minute pellet of earth, which it lays in position and cements with its saliva. As the rampart grows in height it contracts gradually in circumference and assumes a conical form; finally a roof is added, but if the roof be not complete before conditions become unfavourable for work, the orifice is left open above but blocked up at the base of the crater until next evening, to prevent the entry of enemies or rain. The wall and roof are at first very thin, consisting of a single layer of the pellets brought up from underground by the workers. It is, moreover, porous, small interstices being left in a fairly regular arrangement between the pellets. Behind each pore a soldier is on guard. If the observer waves a hand within a few inches of the surface, a kind of shudder passes over the whole structure. This is due to the fact that, as the hand approaches each pore, the soldier behind it thrusts out his head and snaps his jaws. As the soldiers are blind they must either act in response to movements of the air or changes of temperature or else be guided by some such sense as that of smell. They cannot see the possible aggressor.

The process of construction can be observed most easily by breaking down a part of the mound in dull, damp weather. The workers near the breach at first retreat but the soldiers remain, snapping their jaws. Then, in a few minutes, a crowd of workers and soldiers wells up from below. All is apparent confusion, but imperceptibly the soldiers take up their position round the aperture, each with its jaws pointing outwards and its soft body under cover. Each of the workers carries in its jaws a pellet of earth, which it deposits in exactly the right place, secreting a little drop of saliva upon it as it does so. Thus the new wall rises rapidly as a fragile shell, and as it rises, more and more soldiers come on guard, one behind every little pore it contains. Should the new roof have too wide a span to be constructed without support, a pillar rises simultaneously from below to meet it, built by other workers. The whole work is perfectly co-ordinated, but there is no apparent reason how or why the little blind, hurrying workers produce between them a perfect whole. Once the outer shell is complete, or even before its higher parts are finished, workers begin to strength-

⁽¹⁾ The chief of these, at any rate in eastern peninsular India, is the larva of the tiger beetle, *Cicindela hæmorrhoidalis*, which always burrows in the walls of termite-mounds.

en and thicken it from within, depositing more earthen pellets inside the first outer layer. The soldiers still remain on guard, however, and the wall is built round them, leaving each in a little cavity with an opening on both the outer and the inner surface. In the outer walls of the hollow buttresses of the mound of oculatus these little sentry-boxes remain even when the whole structure is complete. The external opening of each is finally closed by a

thin film of earth, so thin that it is often quite translucent.

This is what takes place in damp weather. When repairs become necessary in dry weather the wall is built thicker from the beginning and there are no pores left for the soldiers. When the mound has to be enlarged or altered, the old wall is eaten away from within by the workers and a new one constructed in the manner described, but I have noticed on Barkuda Island in the Chilka Lake that in years in which the monsoon rainfall is scanty or late very little reconstruction takes place and repairs are reduced to a minimum. In years of scanty rainfall, moreover, few new mounds are built.

The building of the termite mound is a subject which I would commend to the attention of any naturalist in search of something to study. There are many points still obscure which could be cleared up with a little application by any careful observer who lived in a country where these mounds were

abundant.

We will have time to-night to consider only one further aspect of the mound, namely the cultivation of fungi in it. In each garden-chamber, as I have already pointed out, there is a spongy mass formed of a brownish material. This consists of the excrement of workers which have been feeding on wood or other vegetable matter. It remains damp in suitable conditions and is disposed in such a way as to form numerous small cells or chambers, which are usually of an oblong shape. On the analogy of the honeycomb the structure is called a fungus-comb, but the resemblance is remote. The whole of the external surface and the inner walls of the cells are covered with a network of very fine white threads on which numerous little round fruit-like bodies of an intense white colour are scattered. The threads are the mycelia, what we may call (somewhat loosely) the roots, of a fungus, while the round white bodies are peculiar masses of fungus-tissue. They are not in any sense the fruit of the fungus but are known as food-bodies or termite truffles. They seem to be produced in some way almost like galls by the action of the termites, for similar bodies are not known in other fungi, but surprisingly little has been discovered as to their origin (1).

The nature, moreover, of the fungus which produces these bodies is still disputed. Dr. Petch, the great authority in Ceylon, believes that it is a peculiar phase of a mushroom-like species called *Collybia albummosa*, which in certain circumstances undoubtedly arises in the fungus-comb and, piercing the wall of the mound, appears on the surface. This fungus is edible and is often collected on termite mounds for human food. It is found only on the mounds and can always be traced down to combs in which the termites are active. It has been found in association with termites in many tropical countries but in comparatively dry localities appears seldom, only when the rainfall is

unusually heavy.

Under all conditions of artificial culture, however, an entirely different fungus springs up from the combs. If they are removed from the nest and placed under a bell-jar on damp blotting-paper numerous little white processes appear, apparently from the network of mycelia, after a few days. These gradually become consolidated into black, fibrous, bodies like leather bootlaces, which are

⁽¹⁾ An interesting parallel is to be found in the cultivation of fungi by certain American ants. See Wheeler's Ants, chap. XVIII, p. 318 (New York: 1910).

the fruit of an entirely different kind of fungus, called Xylaria nigripes. This fungus is also peculiar to termite mounds and whenever found in nature can be traced to deserted combs. It has also a wide range in the tropics in association with various species and genera of termites. It differs, however, from the mushroom-like Collybia in that it appears only after the termites have been removed or died in the comb. Dr. Petch regards this Xylaria of which allied species are often found growing on dead wood, as a mere weed which the termites are unable to eradicate completely from their gardens, though they keep it under control as long as they are active themselves; while he accepts the Collybia as the actual reproductive body of the mycelia on the combs; but the evidence he brings forward is indirect and the matter must still be considered as obscure. To me it appears as if the Xylaria grew directly from the mycelia in the cells.

The same system of cultivation, whatever it may be, is apparently followed by some termites which are mere burrowers and do not build mounds, but their combs are always few and small and rarely if ever have the same complexity of structure as those of the mounds. Sometimes, indeed, they are little more than masses of excrement with imperfectly formed depressions on their surface, whereas in *Odontotermes* at any rate the combs have a "cellular" structure from the beginning of their formation. The cultivation of the mound-builders is thus more highly developed in every respect than that of the burrowers.

We know nothing of how the termites cultivate the fungus or fungi, and very little of why they do so. It has been assumed rather than proved that they eat the food-bodies produced by it, but these bodies certainly do not form the main sustenance of the workers, which have a great majority in the population of the mound. The very existence of the combs proves, indeed, that this is not the case, for they are formed of the excrement of the workers and contain the woody fibres of the substances onwhich the workers feed. Moreover, the workers of many mound-builders make long excursions from the mound in search of dead wood and other decaying vegetable substances. I have known them go over eighty yards to feed on dead weeds at the edge of the Chilka Lake. They approached these weeds from the nest partly by underground passages and partly by little road-ways on the surface which they roofed in with a fragile covering of clay, as is their custom when foraging above ground.

It is certain that the eggs are removed to fungus-combs soon after they are laid, and that the combs near the royal chamber are frequently full of young insects. It seems probable, therefore, that the young termites feed on the food-bodies, which may also be carried by the workers to the king and queen in their royal prison-chamber. The winged adults also remain in the combs, awaiting favourable weather to emerge often for some weeks after their

metamorphosis.

This is all that I can say profitably to-night about termite mounds, but I would again invite your attention to the many interesting problems they offer to the naturalist.

SOME REFERENCES.

Annandale, N.	••	••	"The Habits of the Termites of Barkuda." Rec. Ind. Mus. XXV, pp. 233-252, pls. v, vi
Bose, S. R.	••	••	(1923). "The Fungi cultivated by the Termites of Barkuda." Rec. Ind. Mus. XXV, pp. 253-258
Doflein, F.	••	••	pl. vi (1923). "Termite Truffles." Spol. Zeyl. III, pp. 203-209 (1906).
ESCHERICH, K.	••	••	Termitenteben auf Ceylon, 3 pls. and many text-figures (Jena: 1911).

Несн, Е			Les Termites, one plate, 460 figs. in text (Brus-
			sels: 1922).
HOLMGREN, N.	• •	• •	"Termitenstudien. 1 Anatomische Unterschun-
			gen." Kungl. Svensk. VetenskAkad. Handl.
			XLIV, No. 3, pp. 1-215, 3 plates and many
			text-figures (1909).
,,			"Termitenstudien. 2. Systematik der Termiten."
			Kungl. Svensk. VetenskAkad. Handl.
			<i>XLVI</i> , No. 6, pp. 1-86, 6 plates (1911); 3
			ibid. XLVIII, No. 4, pp. 1-166, 4 plates and
			many text-figures (1912).
,,			"Termites from British India (Bombay) col-
			lected by Dr. J. Asmuth, S.J." Journ.
			Bombay Nat. Hist. Soc. XXI, pp. 774, 793,
			plates A-D (1912-1913).
,,	• •		Monographie der Termiten der Orientalische
			Region (1913).
**	• •	• •	"Termites from British India (near Bombay in
			Gujrat and Bangalore) collected by Dr. J.
			Asmuth, S.J." Journ. Bombay Nat. Hist.
			Soc. XXII, pp. 101-117, plates E. G. (1913-
T 4 T			1914).
Imms, A. D.	• •	• •	"On the Structure and Biology of Archoter-
			mopsis, together with Descriptions of New
			Species of Intestinal Protozoa, and General
			Observations on the Isoptera "Phil. Trans.
			Roy. Soc. 209 B, pp. 75-180, pls. 3-10, and
'IZ			many text-figures (1920).
Kent, W. S.	• •	• •	The Naturalist in Australia, chap. IV "Ter-
			mites (White Ants), pp. 102-131, pls. xv-xxii,
Dramour T			many text-figures (London: 1897).
Ретсн, Т	• •	• •	"The Fungi of certain Termite Nests," Ann
			Roy. Bot. Gard. Peradeniya, IV, pp. 185-270 pls, v-xxi (1906).
,, ••	• •	• •	"Termite Fungi: a Resumé," Ann. Roy. Bot. Gard. Peradeniya V, pp. 303-341 (1913).
			oura. 1 eraaeniga v, pp. 503-541 (1915).